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THE VELIGER

The Nudibranch Genera *Onchidoris* and *Diaphorodoris* (Mollusca, Opisthobranchia) in the Northeastern Pacific

by

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Abstract. An anatomical review was conducted on the genus *Onchidoris* in the northeastern Pacific. Comparisons were based on the published literature and specimens obtained from both the North Atlantic and North Pacific oceans. *Onchidoris muricata* (Müller, 1776) occurs in both the Atlantic and Pacific oceans, and *O. varians* (Bergh, 1878) and *O. hystricina* (Bergh, 1878) are junior synonyms of this species. The nudibranch commonly considered in California to be *O. hystricina* was an unnamed species belonging to the genus *Diaphorodoris*. This new species, *D.* ***lirulatocauda,*** is described and compared with other species in the genus, including *Diaphorodoris* ***mitsuii*** (Baba, 1938) comb. nov. The relationships of the genus *Diaphorodoris* with other genera in the family Onchidorididae are discussed.

INTRODUCTION

FOUR SPECIES OF *Onchidoris* have been reported from the northeastern Pacific. The species *Onchidoris bilamellata* Linnaeus, 1767, and *O. muricata* Müller, 1776, have also been recorded from both sides of the Atlantic (THOMPSON & BROWN, 1976). *Onchidoris hystricina* (Bergh, 1878) and *O. varians* (Bergh, 1878) were described from the northeastern Pacific as cognate species of *O. muricata*. ABBOTT (1974) suggested that both these species are synonyms of *O. muricata*. Unfortunately, the type material is lost (Zoologisk Museum, Copenhagen, personal communication), and comparisons must therefore be made on the basis of the literature.

Three species of *Onchidoris* are found in British Columbian waters. *Onchidoris bilamellata* is easily recognized due to its mottled brown (rarely white) coloration and its unique habit of preying on barnacles. Another species is identical to the Californian species commonly referred to as *O. hystricina*. The third species is of the type referred to as *O. muricata* by BEHRENS (1980:67). An anatomical investigation of the latter two species was undertaken and comparisons made with *O. muricata* of the Atlantic and the literature.

Onchidoris muricata (Müller, 1776)

Doris aspera Alder & Hancock, 1842.
Doris diaphana Alder & Hancock, 1845.
Doris pallida Agassiz, 1850.
Doris ulidiana Thompson, 1845.
Lamellidoris varians BERGH, 1878:613–614; BERGH, 1879: 365; BERGH, 1880a:216–219, pl. 11 (figs. 13, 14); BERGH, 1880b:67–70, pl. 11 (figs. 13, 14), pl. 13 (fig. 1); BERGH, 1890:985; BERGH, 1892:1153 (161); *syn. nov.*
Lamellidoris hystricina BERGH, 1878:605, 614, pl. 68 (figs. 17–23); BERGH, 1879:365; BERGH, 1880a:219–221; BERGH, 1880b:70–72; BERGH, 1890:985; BERGH, 1892: 1153 (161); *syn. nov.*
Onchidoris hystricina (Bergh, 1878): MARCUS, 1961:28, 57, pl. 5 (figs. 89–91).

External morphology: I examined preserved specimens from Norway which ranged in length from 4 to 11 mm, from the Atlantic coast of the United States with lengths of 4 to 10 mm, and from British Columbia, Canada, from 1 to 10 mm in length. Most animals were 5–7 mm long. The body shape is oval, slightly wider and more truncate in front, with a low arch (Figure 1A). A small mantle margin overhangs the sides and foot. The mantle becomes disproportionately larger as the animal's size increases. The notum is covered with rounded tubercles, flattened and uneven on top, constricted at their bases, giving them a mushroom shape.

The tubercles are large, with a few, scattered, small tubercles. Towards the mantle edge all of the tubercles are small. The tubercles of specimens from the Canadian Pacific, Atlantic, and Norwegian Sea had the same average tubercle size. The larger tubercles of specimens from

these three areas were 0.51–0.56 mm high and 0.59–0.65 mm wide at the top.

Spicules run lengthwise in the tubercles (Figures 1B, 2A, B) and are capable of being protruded through openings in grooves along the flattened top (KRESS, 1981, figs. 5E, F). In a relaxed state the spicules do not protrude and the tubercle is an inflated mushroom shape. When contracted, the tubercles appear cylindrical with flattened spiculose tops. Short spicules radiate in a star-like pattern in the notum at the tubercle bases. In the notum there is a dense spicule arrangement that shines through the integument in a cross, transverse, circular, radiating pattern as diagrammed by ALDER & HANCOCK (1855, pl. 48 [fig. 2]). The margins of the rhinophores bear 2 (sometimes 3) tubercles, and there are 3 to 8 tubercles inside the branchial circlet, which is located on the posterior midline.

The simply pinnate, contractile gills are separate, arranged in a nearly complete, transverse oval, broken midposteriorly by the post-anal tubercle. Gill number varies between 6 and 18 in Pacific specimens, 8 to 14 in Atlantic specimens. The anterior-most gills are the largest, decreasing gradually in size toward the posterior.

The rhinophores are long and slender with a rectangular, flat-topped tip. The stalk is short, and most of the clavus has long sloping lamellae. The lamellae, except for the most distal one, are attached along the anterior line. Posteriorly only the first 3 or 4 are complete, with an ever-widening bare space proximally. Atlantic specimens had 9 to 20 lamellae, Pacific specimens had 6 to 10. The rhinophore margin is not raised and is smooth except for 2 (sometimes 3) tubercles which are positioned on either side of the anterior border.

The head has a semicircular velum, usually with folds to mark the triangular tentacles that are attached posteriorly.

The large foot is truncate anteriorly, thickened but not bilabiate. The foot is wider in front than behind and ends in a bluntly rounded tail which is covered by the mantle margin.

Living Pacific specimens were usually white, occasionally creamy-white, light yellow, or light orange. The notum is semitranslucent. Through it can be seen the bright red digestive gland, which in mature specimens becomes obscured by creamy gonads. In mature animals, a dark brown spot, the sperm-filled bursa copulatrix, can be seen through the anterior right side of the dorsum. Ventrally, the red digestive gland shows clearly for ⅔ of the body length. It extends farther forward on the left side. The leaves of the rhinophores are dusky yellow or orange. The branchiae are lighter than the body, white or dusky yellow with an opaque white base. A color photograph appears in BEHRENS (1980:fig. 72). Atlantic specimens are either white or pale yellow, the latter color being more common at the northern end of its range (THOMPSON & BROWN, 1976).

Digestive tract and radula: The internally folded buccal tube is short, broad, and flaccid. The buccal bulb has a dorsal rounded sucking crop with a broad median muscular band and a short stalk. The radular sac projects posteriorly. It is long, cylindrical, and usually bent to one side. The lip disk has been described as having a thick yellowish cuticle (BERGH, 1880).[1] With the aid of the scanning electron microscope, I found the lip disks of Atlantic and Pacific specimens to be finely papillate toward the central area. The opening is guarded by two ventral flaps (Figure 1C). The lip papillae were illustrated by BERGH (1878, pl. 68 [fig. 17]) for *Onchidoris hystricina,* and reported by BERGH (1880) in *O. varians.*

Atlantic specimens of *Onchidoris muricata* have been reported to have radulae ranging in length from 29 to 44 rows. I found that specimens from the Atlantic have from 27 to 34 rows and specimens from the Pacific have 20 to 33 rows.

The radula is narrow, with the formula 1.1.1.1.1 (Figure 1D). The central (rachidian) tooth is an elongate rectangular shape with thickened sides. In Atlantic specimens of *Onchidoris muricata* its length was 0.05 mm (BERGH, 1880). Specimens that I examined from the Atlantic had central-tooth lengths of 0.03–0.04 mm ($\bar{X}$ = 0.04 mm; n = 9) and from the Pacific 0.02–0.06 mm ($\bar{X}$ = 0.04 mm; n = 25).

Each large lateral tooth (Figure 1D) has a triangular-shaped base with a denticulate hook. At the base of the denticulations is a knoblike projection from which a small wing extends down the inner side of the tooth. Reported tooth height for *Onchidoris muricata* is 0.075–0.12 mm (BERGH, 1880; MEYER, 1971). My specimens from the Atlantic had a tooth height of 0.07–0.10 mm ($\bar{X}$ = 0.08 mm; n = 8) and from the Pacific 0.04–0.10 mm ($\bar{X}$ = 0.08 mm; n = 16). Bergh did not measure the lateral tooth height of *O. hystricina* but reported them to be smaller than the 0.12–0.17 mm he found in *O. varians,* although of the same shape (see Figures 9C, D). The number of denticles varied in Atlantic *O. muricata* from 9 to 16 and in Pacific specimens from 8 to 18. There was substantial variation in the strength of denticulation and the numbers of denticles. Older, worn teeth had the tips of the hooks ground away and the denticles extended almost to the tip as in *O. varians.* Younger teeth had a longer, straighter, smooth cusp with denticles only near the base as in *O. hystricina.*

The marginal teeth have a triangular base with a single strong recurved hook facing posteriorly (Figure 1D). *Onchidoris muricata* from the Atlantic had a marginal tooth height of 0.04 mm (BERGH, 1880). Atlantic specimens that I examined had a height of 0.03–0.04 mm ($\bar{X}$ = 0.03 mm; n = 9), while those from the Pacific had a tooth height of 0.02–0.05 mm ($\bar{X}$ = 0.03 mm; n = 19).

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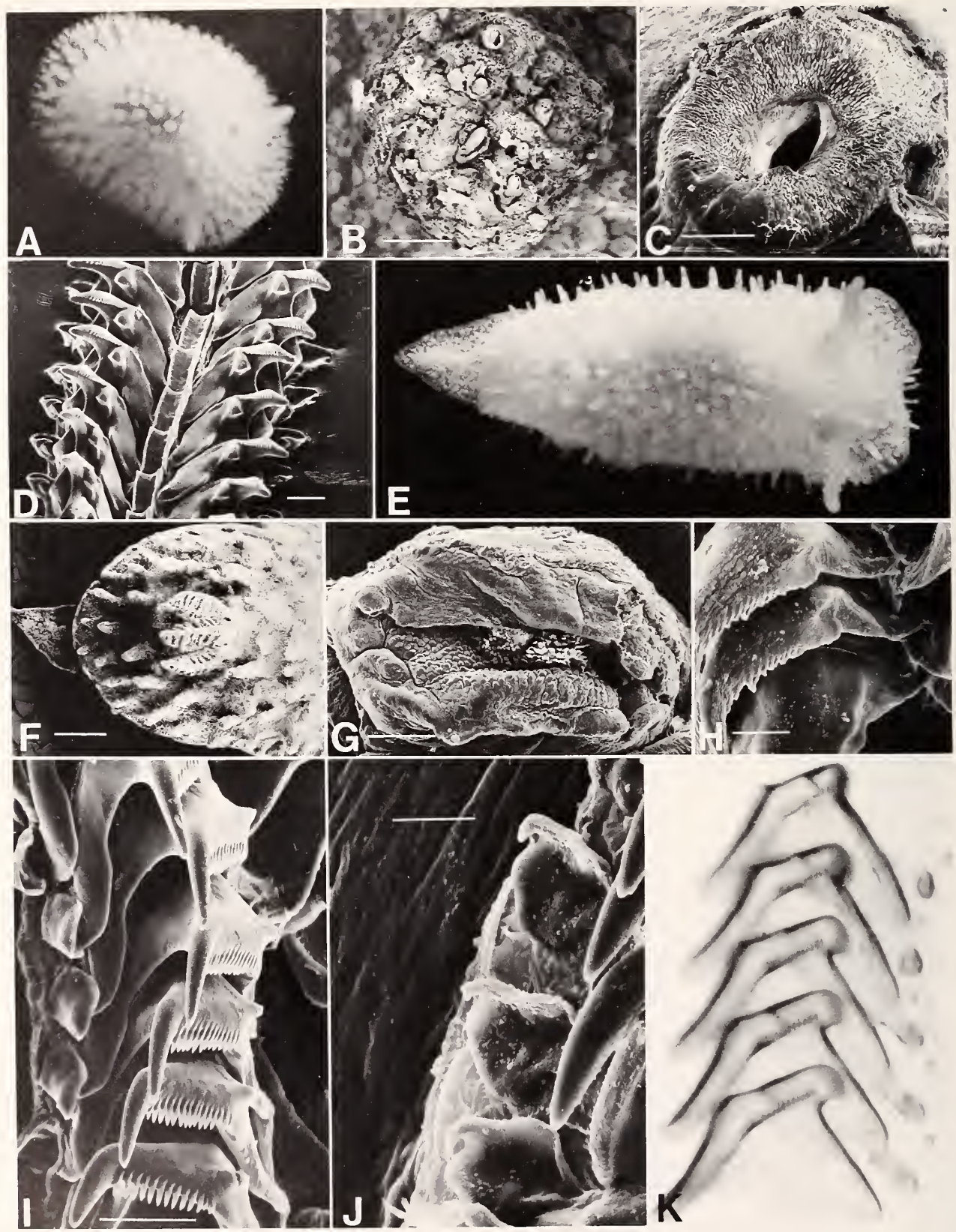
[1] Text references to BERGH (1880) refer both to BERGH (1880a) and (1880b) listed separately in the Literature Cited. They are the same paper published in two different journals.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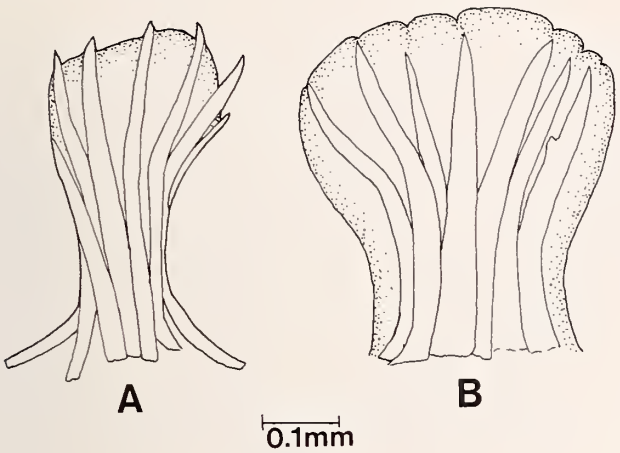

Figure 2

Tubercles of *Onchidoris muricata* showing the arrangement of the spicules. A. Contracted state. B. Relaxed state.

At the posterior end of the buccal bulb is a narrow tubular esophagus. The salivary glands are attached on either side of the base of the esophagus. BERGH (1880) described them as 2 or 3 thick, white coils in *Onchidoris muricata,* and as a large, whitish mass in *O. varians.* I found them to be small and U-shaped in both Pacific and Atlantic specimens. The stomach is buried in the digestive glands except at the junction of the intestine, where a small, round, stalked caecum is given off. The digestive glands appear as one oval reddish mass hollowed on the anterior right due to the reproductive organs. The narrow tubular intestine loops to the right around or over the caecum and runs straight to the anus, located at the posterior of the branchial circlet at the base of a large tubercle. The anal opening is simple and not raised. The inconspicuous renal pore is located within the circlet to the right of center, surrounded by tubercles.

Circulatory system: The pericardial sac contains a posterior, thin-walled, triangular auricle and a ventricle. The aorta ends in a large, granular, white, blood gland situated above the central nervous system.

Central nervous system: The central nervous system has been well described for *Onchidoris muricata* by BERGH (1880). He also described and illustrated this system for *O. varians* (pl. 13 [fig. 1]) and described it for *O. hystricina.* In all three species the cerebral and pleural ganglia are fused, ovate or rounded, and connected by a short commissure. The almost separate pedal ganglia are rounded and only slightly smaller than the cerebro-pleurals. The eyes are on moderately long, fine stalks. There were no discernible differences in this system in specimens from the Atlantic or the Pacific.

Reproductive system (Figure 3): The ovotestis consists of creamy-yellow lobules on the dorsal surface, sides, and part of the ventral surface of the digestive glands. Its histology and maturation have been studied by BEHRENTZ (1931) and TODD (1978a). The branched gonoducts of the ovotestis merge forming a thin pre-ampullary duct. This duct widens into a U-shaped ampulla, which is attached to the inner, lower curvature of the albumen gland. It narrows to form a thin post-ampullary duct, which ends at a triple junction. One branch becomes the vas deferens, another leads to the buried receptaculum seminis (fertilization chamber), and a third, the short oviduct, enters the female gland mass. The vas deferens is narrow and prostatic for a short distance. It becomes non-prostatic, looping dorsally, then enlarging into a muscular penial sac. Inside, the vas deferens coils and then straightens, ending in an unarmed, simple, bifurcate or trifurcate penis.

The vagina, which is short and muscular, has a separate opening posterior to the penial sac. The vagina leads to a bluntly rounded, blind sac, where on one side the moderately long duct to the large round bursa copulatrix is given off. The fertilization duct is long, muscular and convoluted, terminating in a buried, oval receptaculum seminis. The arrangement of the ducts is semiserial.

The female gland mass has a separate nidamental duct ventral to the vagina. This mass has an anterior, yellowish, albumen gland and a posterior, inner, mucous gland. The receptaculum seminis is buried in the albumen gland.

The reproductive openings are located on the right side a short distance posterior to the anterior margin of the foot.

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Figure 1

A. *Onchidoris muricata,* 7 mm. Photograph of a live Pacific specimen. B. Tubercle of *O. muricata,* SEM micrograph of a Pacific specimen. Scale = 100 μm. C. Lip disk of *O. muricata,* SEM micrograph of an Atlantic specimen. Scale = 100 μm. D. Radula of *O. muricata,* SEM micrograph of a Pacific specimen. Scale = 40 μm. E. *Diaphorodoris* ***lirulatocauda,*** 12 mm. Photograph of a live specimen. F. Posterior half of *D.* ***lirulatocauda*** showing tubercles and gills. SEM micrograph. Scale = 1 mm. G. Lip disk of *D.* ***lirulatocauda,*** SEM micrograph. Scale = 50 μm. H. Radula of *D.* ***lirulatocauda,*** SEM micrograph of medial area showing connecting membranous wing of laterals. Scale = 10 μm. I. Radula of *D.* ***lirulatocauda,*** SEM micrograph of lateral and first marginal teeth. Scale = 20 μm. J. Radula of *D.* ***lirulatocauda,*** SEM micrograph of inner marginal teeth. Scale = 10 μm. K. Radula of *D.* ***lirulatocauda,*** light microscope photograph of one half row including reduced outer platelet.

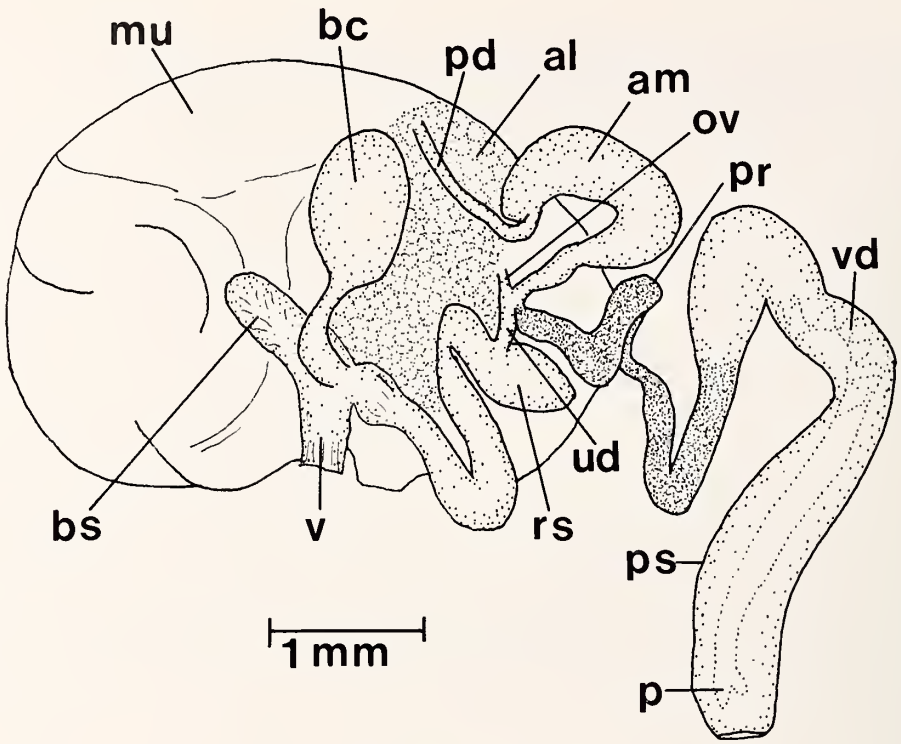

Figure 3

Onchidoris muricata reproductive system, drawn using a camera lucida. Key: al, albumen gland; am, ampulla; bc, bursa copulatrix; bs, blind sac; mu, mucous gland; ov, oviduct; p, penis; pd, preampullary duct; pr, prostate; ps, penial sac; rs, receptaculum seminis; ud, uterine duct; v, vagina; vd, vas deferens.

This system was found to be essentially the same for Atlantic and Pacific specimens. It agrees with the description given for *Onchidoris muricata* by BERGH (1880) and with his partial descriptions for *O. varians* and *O. hystricina*. It should be noted that Bergh did not consider the vas deferens (spermatoduct) of *O. hystricina* to be very long. The reproductive system was reconstructed by BEHRENTZ (1931, figs. 6–9) using serial sectioning. Behrentz noted that the penis has three "horns." On specimens of *O. muricata* that I examined, the penis was often a simple cylinder or showed two lobes.

Ecology: *Onchidoris muricata* occurs in the low intertidal zone and shallow subtidal to 20 m (THOMPSON & BROWN, 1976). It ranges from the White Sea to Cape Finisterre, Greenland, from Nova Scotia to Rhode Island in the Atlantic, and from Kyska, Alaska, to California in the Pacific. The southern range limit is uncertain due to confusion with the next species and an undescribed *Adalaria* species. I examined specimens from as far south as Abalone Beach, Humboldt County, California and MARCUS's (1961) specimen came from Dillon Beach, California.

In Britain this species eats a variety of encrusting bryozoans, especially *Electra pilosa, Membranipora membranacea,* and *Alcyonidium polyoum* (THOMPSON & BROWN, 1976; TODD, 1978b, 1979a, 1981). In the Pacific it also eats a variety of encrusting bryozoans, most of which are cheilostomate. Specimens have been reported feeding on *Reginella mucronata, Eurystomella bilabiata,* and *Microporella cribosa* (MCDONALD & NYBAKKEN, 1978; GODDARD, 1984). In British Columbia the species feeds most often on *Schizoporella unicornis* but has also been found on *Hippodiplosia insculpta, Cheliopora praelonga, Lagenipora* sp., *Microporina borealis,* and *Membranipora serrilamella* (personal observations). It feeds by sucking the bryozoan polypides out of their skeletons, approximately 19–32 polypides being eaten per adult per day (TODD, 1979a, 1981) at a rate of 0.4–5.2 polypides per hour (TODD, 1979b, 1981). The nudibranchs are normally found on rocks and under boulders. TODD (1978b) found that their distribution on the undersurface of boulders showed aggregation, which was particularly pronounced during breeding season.

The life cycle has been studied in Sweden (BEHRENTZ, 1931) and in Britain (THOMPSON, 1961b; MILLER, 1962; TODD, 1979a, b, 1981). In both places this species was an annual, settling in the summer, growing until the early spring, when animals over 3 mm spawn. Spawning animals die in June, leaving a brief interval between gener-

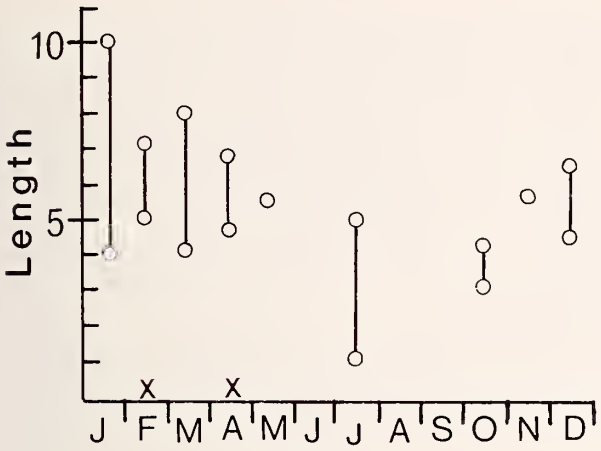

Figure 4

Onchidoris muricata. Annual cycle of Pacific animals. Preserved length in mm versus month collected. Spawn present in months marked "x." n = 91.

ations. Specimens collected from British Columbia (Figure 4) had a similar annual cycle.

The spawn mass is white or pale orange in 1½–2 whorls. The eggs are in a string folded up and down in the whorl, although this pattern is not obvious. The egg mass is quite thick and leans inward. The eggs are usually found one to a double-walled capsule. The eggs are 75.0–77.3 μm (Goddard, 1984), 73–100 μm (Thompson, 1967), or 80–100 μm (Todd, 1979b) in diameter, with a capsule size of 99–117 μm (personal observation). There are approximately 2500 eggs/ribbon (Thompson, 1967; Todd, 1978a). Each animal lays approximately 15,000–34,000 eggs in its lifetime (Todd, 1979b). Egg masses are produced in a regular 4–5 day cycle, with mating necessary prior to each spawning (Todd, 1978b).

The eggs hatch in 7–20 days (Miller, 1958; Thompson, 1967; Hurst, 1967; Goddard, 1984; personal observations) into Type-1 veligers of Thompson (1967), with shell Type 1 (Thompson, 1961a) and having a length of 117–136 μm (Goddard, 1984; personal observations). The larvae are long-term planktotrophs with a larval life estimated at 12 wk (Behrentz, 1931) or 7–8 wk (Todd, 1979a, b). I maintained larvae, fed on phytoplankton, in the laboratory at 8°C for 7 weeks, when they suddenly died without metamorphosing. This corroborates Todd's estimate. Animals in Britain preferentially settle on the bryozoan *Callopora aurita* even though as adults they prefer *Electra pilosa* (Todd, 1979a, b, 1981). Adult animals are quite active compared to other dorid nudibranchs and have the disconcerting habit of crawling out of their dish and drying up on the sides when kept in the laboratory.

Diaphorodoris ***lirulatocauda*** Millen, spec. nov.

Onchidoris hystricina (Bergh, 1878): Beeman & Williams, 1980:328 (section 14.42), pl. 105 (fig. 14.42) (*non* Bergh); Behrens, 1980:66–67 (fig. 71) (*non* Bergh); McDonald & Nybakken, 1981:16, 31, 44–45 (fig. 18) (*non* Bergh); Nybakken & McDonald, 1981:440, 442 (fig. 1H) (*non* Bergh); McDonald, 1983:198–199 (fig. 36) (*non* Bergh); Jaeckle, 1984:209 (*non* Bergh).

Onchidoris sp. (cf. *Onchidoris hystricina*): Goddard, 1984: 143–163.

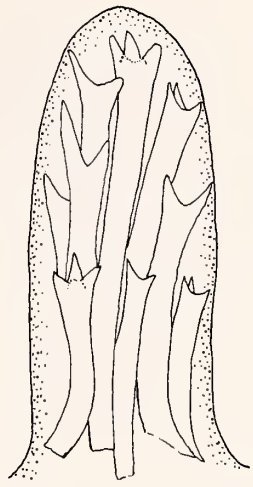

Figure 5

Diaphorodoris ***lirulatocauda*** tubercle showing the arrangement of the spicules.

Material: Holotype: British Columbia Provincial Museum, BCPM-984-347-1, 5 June 1979, Earls Cove, British Columbia, Canada (49°45′N, 124°01′W), 20 m depth, rocky substrate on bryozoans growing on *Rhabdocalyptus dawsonii,* spawning, coll. S. Millen.

Paratypes: In the British Columbia Provincial Museum three lots: BCPM-976-1037-6, 27 Mar. 1976, Juan Perez Sound, Queen Charlotte Islands, British Columbia, Canada (52°35.8′N, 131°25.2′W), 10–20 m, rock with coralline algae, 3 specimens, coll. P. Lambert; BCPM-976-1057-5, 18 June 1976, Arbutus Island, British Columbia, Canada (48°42.4′N, 123°26.1′W), <13 m, rocky substrate, 4 specimens, coll. P. Lambert; BCPM-976-1073-10, 2 Aug. 1976, Discovery Passage, British Columbia, Canada (50°19.7′N, 125°26.4′W), <25 m, rock with hydroids, 6 specimens, coll. P. Lambert. In the California Academy of Sciences two lots: CASIZ 031680, 8 Aug. 1968, Hazard Canyon, San Luis Obispo Co., California, 1 specimen, coll. D. Roller; CASIZ 031682, 8 Aug. 1964, Moss Beach, California, 1 specimen, coll. L. Andrews.

Etymology: The name ***lirulatocauda*** is derived from the Latin *lirulatus,* meaning "ridged," and *cauda,* meaning "tail," and refers to the mid-dorsal ridge on the tail. This feature distinguishes this species from similar small white dorids in the family Onchidorididae.

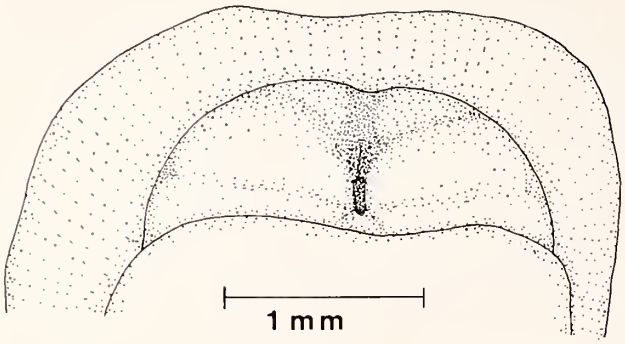

Figure 6

Head of *Diaphorodoris* ***lirulatocauda.***

External morphology: I examined 44 specimens from British Columbia and California ranging in length from 3 to 12 mm. The body shape is elongate-oval (Figure 1E), wider in front than behind, with a trailing, keeled tail. The mantle margin is not wide, but covers the high sides and is slightly longer in front, covering the head. The notum bears elongate, slender, cylindrical tubercles with blunt but not inflated ends. The tubercles taper slightly from their bases. They are soft and capable of slight contraction. The tubercles show little variance in size, although smaller tubercles predominate toward the mantle edges. They are spaced fairly far apart, not crowded. In some specimens, the tubercles appear to form longitudinal rows. Larger tubercles are from 0.34 to 0.64 mm high and 0.13 to 0.28 mm wide.

Spicules are found in the tubercles, but they do not protrude, even when the tubercle contracts (Figure 1F). The spicules are densely packed in the central core of the tubercles and have trifurcate ends (Figure 5). At the bases of the tubercles the spicules extend in a radial, star-like pattern through the notum. In the notum there are large, curved spicules with side prongs and slightly smaller S-shaped spicules scattered in the connective tissue. These spicules do not form a definite pattern, nor are they visible in living animals. In the foot, the spicules form a crisscross pattern. The margins of the rhinophores bear three tubercles, two anterior and one posterior. There are no tubercles within the branchial circlet. The branchial margin is smooth except for one large posterior tubercle, but several slightly smaller tubercles are sometimes present (Figure 1F).

The simply pinnate, contractile, branchiae are non-retractable, enclosed in a common sheath, and joined at their bases. There are 4–9 gills, the most anterior being the longest and the most posterior two being very small.

The rhinophores are long and slender, with a long, blunt tip. The stalk is long and most of the clavus bears sloping lamellae. The 6–10 lamellae are attached along a vertical, anterior line, except for the most distal one or two. The lamellae slope ventrally and meet posteriorly forming a chevron, except for the most proximal two or three which are incomplete.

The head (Figure 6) is rounded, not extended into a large veil, but appearing as a double, rounded mound, separated by the vertical mouth opening. There are small, longitudinal, lateral tentacle grooves.

The foot is narrow and elongate, wider and truncate anteriorly. The anterior foot edge is not bilabiate. Dorsally the protruding tail, which ends in a sharp point, has a medial ridge.

Living specimens are white or creamy-white, with opaque white, granular flecks in the notum, the top of the foot, and head, but not on the tubercles. In mature animals, the mid-dorsal region appears darker yellow due to the creamy gonads underneath. Sometimes there is a brown spot on the anterior right, indicating the location of the sperm-filled bursa copulatrix. Ventrally the dark-brown digestive gland is visible through the foot, although it is often obscured by the creamy-yellow gonads. The rhinophores are creamy-yellow, as are the gills. The gills may have white granulations near their bases and an opaque white line up the central shaft. Color photographs appear in Beeman & Williams (1980: pl. 105 [fig. 14.42]), Behrens (1980:fig. 71), and McDonald & Nybakken (1981: fig. 18).

Digestive tract and radula: The soft buccal tube is surrounded by glands made up of large granules. The buccal bulb has a dorsal, rounded sucking crop which is sessile. The crop has a broad muscular band dorsally, but only a thin muscular strip posteriorly. On the ventral surface a small radular sac projects posteriorly. The lip disk is smooth, except in the central passageway, where it has small, oval papillae that are 7–8 μm in diameter (Figure 1G).

The radula has 29–33 rows. The radular formula is 2.1.0.1.2, with no central (rachidian) tooth. A membranous wing runs from the inner posterior corner of each lateral tooth to join just inside the inner base of the following tooth (Figure 1H). The large lateral teeth (Figure 1I) have a wide triangular base with a small, needlelike recurved hook. At the inner base of the hook extends a comblike row of 11–13 denticles. Above and inside the row of denticles is a prominent knob. The lateral teeth range in height from 0.05 to 0.06 mm. The innermost marginal tooth has an oval base with a posterior-facing middle hook (Figure 1J). The height is 0.02 mm. On the outside of this is a small, insubstantial, oval plate (5–10 μm long), representing a rudimentary second lateral tooth (Figure 1K).

At the posterior end of the buccal bulb is the long, thin esophagus. The salivary glands insert at its base. These are long, thin straps running down the sides of the digestive gland for half its length before bending ventrally. The small stomach is buried in the digestive gland, but a round, short, stalked caecum extends from it to the surface. In

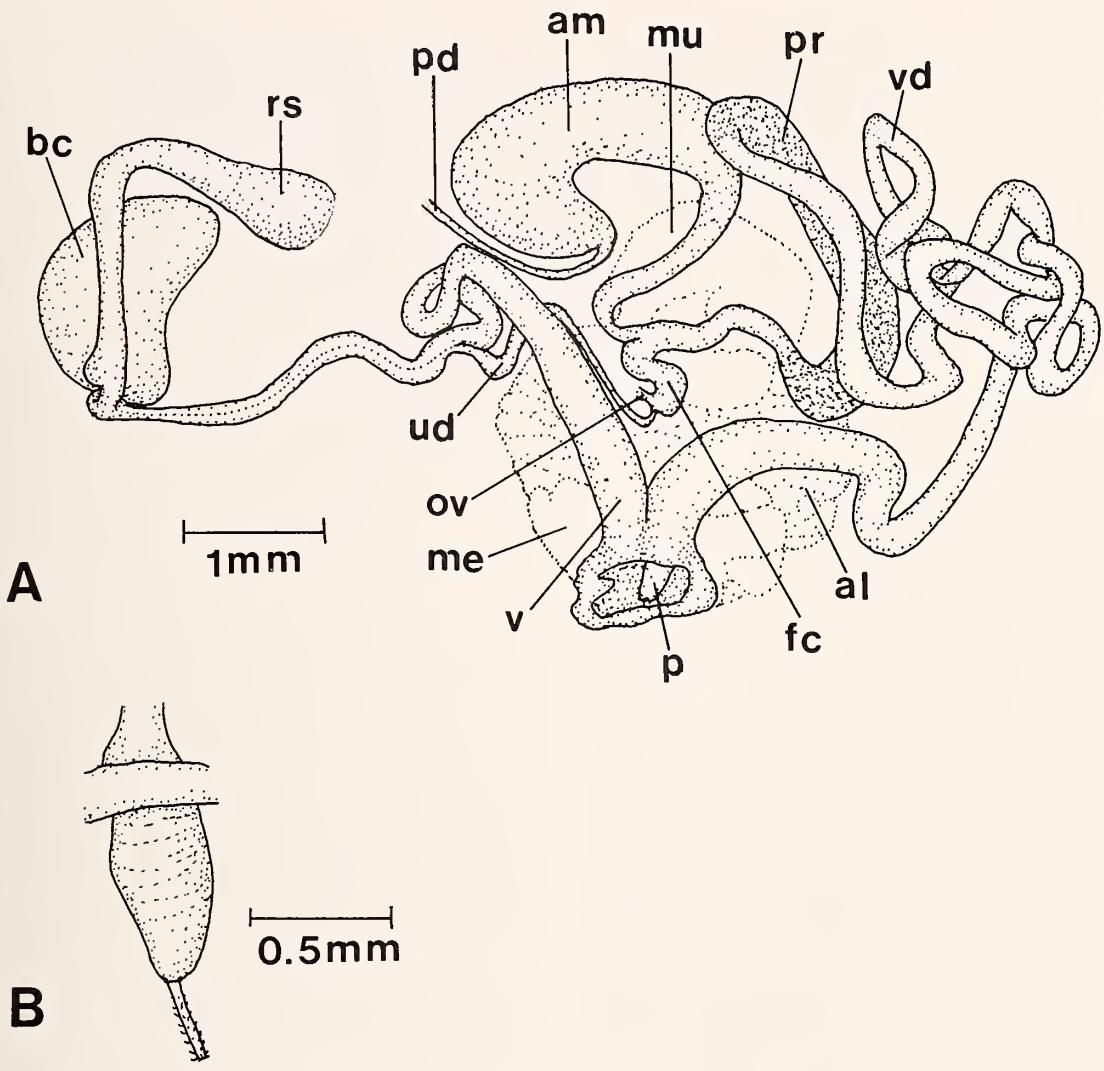

Figure 7

A. *Diaphorodoris* ***lirulatocauda*** reproductive system, drawn using a camera lucida. Key: al, albumen gland; am, ampulla; bc, bursa copulatrix; fc, fertilization chamber; me, membrane gland; mu, mucous gland; ov, oviduct; p, penis; pd, preampullary duct; pr, prostate; rs, receptaculum seminis; ud, uterine duct; v, vagina; vd, vas deferens. B. Conical penis with everted, armed, central core.

mature animals the digestive gland is covered by the gonads. The oval, brown digestive gland appears as one mass. The intestine emerges beside the caecum, curves to the right, and runs as a long, thin tube to the anus, located in the center of the branchial circlet. The renal pore is to the right and slightly anterior to the anal opening.

Circulatory system: The auricle is large, triangular, and thin. The ventricle is small, muscular, and rounded. The muscular aorta ends in fluffy, white, blood glands located just posterior to and slightly over the central nervous system.

Central nervous system: The cerebro-pleural ganglia are fused, large, and elongate oval in shape. The smaller, rounded pedal ganglia are ventrally located and are connected by a short circumesophageal commissure. The olfactory bulbs have a short stalk. The eyes are connected to the cerebro-pleural ganglia by long optic nerves with small bulbs at their bases. The paired buccal ganglia are separated by a short commissure and each has a gastro-esophageal ganglion attached by a short stalk.

Reproductive system (Figure 7): The ovotestes are creamy-yellow lobules entirely covering the digestive gland, including the ventral side. The gonoducts are broad, shiny white and conspicuous, uniting to form a central preampullar duct, which widens into the U-shaped ampulla. This ampulla is attached to the inner side of the female

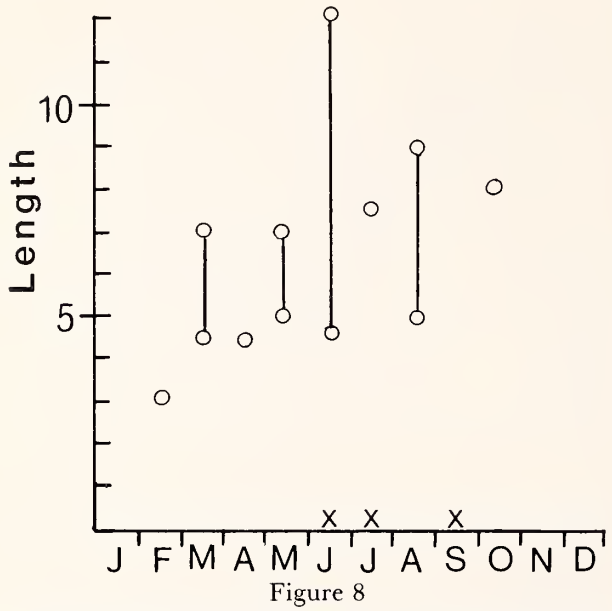

Figure 8

Diaphorodoris ***lirulatocauda.*** Annual cycle. Preserved length in mm versus month collected. Spawn present in months marked "x." n = 40.

gland mass. The post-ampullar duct bifurcates into a short, wide fertilization duct and an extremely long, coiled vas deferens. The inner portion of the vas deferens widens into a soft granular prostatic section, then narrows to a coiling, muscular portion. Near the outer body wall the vas deferens widens slightly to join a common atrium with the vagina. This atrium has a plicate edge. The conical penis is located at the anterior of the atrium, and has a central protrusible core bearing spines. The core, which can extend 300–400 μm, bears approximately 8 irregular rows of 15–25 spines. The spines are simple rods with pointed, downward-tipped ends. They vary in length from 8 to 23 μm, the shortest being most proximal.

The vagina is long and cylindrical, wider near its posterior opening in the atrium and gradually narrowing into a long duct leading to the sessile bursa copulatrix. Just after it narrows, the uterine duct branches off. The vaginal duct beyond this point has a double-partitioned interior. The bursa copulatrix is a large, round thin-walled sac, dark-brown when filled with sperm. At its junction with the vagina, the moderately long duct of the club-shaped receptaculum seminis bends anteriorly. The arrangement of the ducts is vaginal. The uterine duct is combined with the vagina for one-half of its length. It then separates from the vaginal duct and crosses the posterior portion of the female gland mass. It terminates in a slightly swollen fertilization chamber next to the short oviduct, which in turn enters the female gland mass.

The female gland mass consists of a membrane gland, mucous gland, and albumen gland. Its exit is located just ventral to the vaginal opening. A short duct widens into an interior, white membrane gland and then widens further into a more dorsal, yellow, highly convoluted albumen gland. On top of the albumen gland is the soft, granular, white coil of the mucous gland. The oviduct enters the mucous gland at its junction with the albumen gland.

The genital openings are located on the right side, a short distance behind the anterior margin of the foot.

Ecology: The habitat and life cycle of this species has been frequently confused with those of *Onchidoris muricata.* I will therefore restrict my observations to specimens that I have examined. This species occurs in the low intertidal down to 126 m subtidally. It ranges from Juan Perez Sound, Queen Charlotte Islands, British Columbia, to Point Loma, California.

This species has been observed eating the ctenostome bryozoan *Nolella stipitata.* The nudibranchs are usually found under rocks intertidally or crawling on rocky surfaces and sponges subtidally. They have been found from February to October, reaching their largest size in the summer (Figure 8). Spawning has been observed in June, July, and September (GODDARD, 1984; personal observations). The spawn mass and development time have been described by GODDARD (1984). He found the spawn mass to be white, in a sausage-shaped cord laid in a disorderly spiral of 1–4 turns. The single egg per capsule had a diameter of 62.6–64.0 μm and hatched in 9–11 days (at 12–16°C) into Type-1, eyeless veligers of THOMPSON (1967). The veligers have shell Type 1 of THOMPSON (1961a) and a length of 113.3–116.6 μm. The duration of the larval stage is unknown.

DISCUSSION

Synonyms of *Onchidoris muricata*

Onchidoris muricata from the Atlantic has the same internal and external morphology as the animals from the Pacific that are described as *O. varians.* I therefore consider them synonymous. BERGH (1880) distinguished *O. varians* on the basis of its bluish color as opposed to the light yellowish, white, or yellowish-white colors of *O. muricata.* Nevertheless, he conceded that a variety of *O. varians* is yellowish-white or yellowish. The radula formula for *O. varians* is 30–41 × 1.1.1.1.1, with 15–20 denticles reaching to the end of the hook (Figure 9C). This is within the range for *O. muricata* from Norway (Table 1, Figure 9A). Live specimens from the eastern Atlantic are reported to reach a length of 17 mm (BEHRENTZ, 1931), whereas the largest live specimen found on the Pacific coast was 12 mm. When Pacific animals from Vancouver Island were compared with Norwegian animals (Table 1, Figure 9B), the following differences were found. Identically sized specimens were alike, but some larger animals had been collected in Norway. These latter specimens bore disproportionately large tubercles and a similarly oversized mantle margin. They had been labeled *Adalaria loveni*

Table 1

Morphological features of the species of *Onchidoris* and *Diaphorodoris* examined.

	O. muricata	*O. muricata*	*O. hystricina*	*O. varians*	*D. **lirulatocauda***
Location	Atlantic	Pacific	Pacific	Pacific	Pacific
Color	white, yellowish	white, yellowish	bluish, yellowish	bluish	yellowish
Body	oval	oval	oval	oval	elongate
Head	veliform	veliform	veliform	veliform	knobbed
Foot	short	short	short	short	elongate
Branchiae	disk large	disk large	disk large	disk large	disk small
	separate pits	separate pits	separate pits	separate pits	common pit
	8–14	6–18	12	12–20	4–9
Tubercles	knobbed club	knobbed club	clubbed	clubbed	cylindrical
	spicules project	spicules project	spicules project	?	not projecting
Skin	spicules show	spicules show	spicules show	no spicules	spicules buried
Radula	27–44 (1.1.1.1.1)	20–33 (1.1.1.1.1)	40 (1.1.1.1.1)	30–41 (1.1.1.1.1)	29–33 (2.1.0.1.2)
Denticles	9–16 fine	8–18 fine	6–8 fine	15–20 stronger	11–13 very strong
Vas deferens	short	short	short	short	long
Penis	large	large	large	large	small
Receptaculum	buried	buried	?	?	free

(Alder & Hancock, 1862) on the basis of their external anatomy. However, when compared with equal-sized bona fide *A. loveni,* it could be seen that the tubercles of the large Norwegian specimens of *O. muricata* were not as large and were more constricted at their bases. Internally, the single marginal tooth per half row, as opposed to the 8–12 found in *A. loveni,* provided positive identification of these mislabeled animals. The only unexplained difference noted by Bergh for *O. varians* is the lack of spiculation. This was probably an artifact of preservation.

The species *Onchidoris hystricina* has been the object of confusion on the Pacific coast. Bergh (1878, 1880) obtained one specimen that Dall found in Alaska. He separated it from *O. muricata* by its color (bluish rather than yellowish-white). He separated it from *O. varians* apparently because of slight differences in the nervous system, a thinner belt of denticles on the lip cuticle, and smaller lateral plates (0.075 versus 0.12 mm in height). The denticulation on the lateral teeth was weaker, there were fewer denticles (8 versus 20), and the denticles did not extend as far out toward the tip. Bergh did not consider these differences to be great, and he concluded that ". . . the possibility cannot be denied that further investigations may show both the Pacific 'species' to be merely varieties of the old *Lamellidoris muricata* of the Atlantic." *Onchidoris hystricina* is compared with the other two species (Table 1, Figure 9D). The differences noted by Bergh fall within the range of variability of *O. muricata. Onchidoris muricata* can be an almost translucent bluish color, opaque white, or pale yellow. Meyer (1971) reported teeth with a height of 0.075 mm in *O. muricata,* the same height that Bergh found in *O. hystricina.* I found *O. muricata* from Norway with 9–16 denticulations, usually ending before the tip, but at times continuing to the end. Tooth heights varied from 0.057 to 0.090 mm. Younger teeth had longer, straighter hooks; older, worn teeth had shorter, blunter, more curved hooks, much as shown by Thompson (1958: 51, fig. 2) for *Adalaria proxima* (Alder & Hancock, 1854). Bergh's (1879:pl. 68 [figs. 18–23]) drawings of the teeth of *O. hystricina* are consistent with newer, unworn teeth (Figure 9D). I therefore consider *O. hystricina* to be a junior synonym of *O. muricata.*

Misidentification of *Diaphorodoris **lirulatocauda*** and *Onchidoris muricata*

Confusion has arisen in the literature due to the mistaken association of the distinctive new species *Diaphorodoris **lirulatocauda*** with the name *Onchidoris hystricina.* Three factors probably led to this error. Firstly, *O. muricata* had its known range extended to California by Marcus (1961) under the misnomer of *O. hystricina.* Because later researchers realized two species occurred in California, one was correctly identified as *O. muricata*; the other (*D. **lirulatocauda***) was given the name *O. hystricina,* as this was the only other name reported from California for a similar appearing animal. Secondly, both *O. hystricina* and *D. **lirulatocauda*** have tooth denticles that do not extend to the end of their strongly hooked laterals. This reinforced the misidentification even though the lateral teeth differ in shape (Figures 9D, E). Thirdly, the tubercles of *O. hystricina* are mistakenly reported by Bergh (1880) as being 1.2 mm high, which is much higher than the 0.51–0.56 mm actually found in *O. muricata. Diaphorodoris **lirulatocauda*** has slightly longer tubercles than *O. muricata,* and this reinforced its identification with the name *O. hystricina.* However, the longest tubercles of *D. **lirulatocauda*** are only 0.64 mm long, which is not nearly as long as in Bergh's report. When the features of *D. **lirulatocauda*** are compared closely with *O. hystricina* as described by Bergh, many important differences emerge

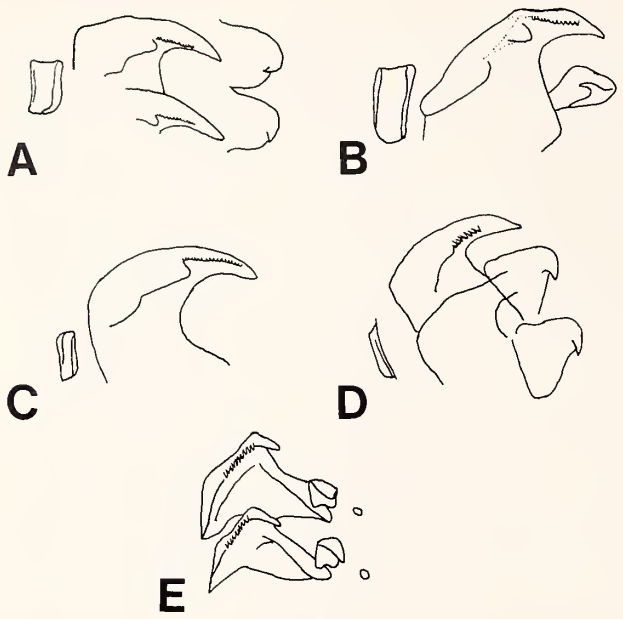

Figure 9

Radular teeth. A. *Onchidoris muricata* (Atlantic) from BERGH, 1880:pl. 11 (fig. 10). B. *Onchidoris muricata* (Pacific). C. *Onchidoris varians* from BERGH, 1880:pl. 11 (figs. 13, 14). D. *Onchidoris hystricina* from BERGH, 1878:pl. 68 (figs. 18, 21). E. *Diaphorodoris* ***lirulatocauda.*** Not drawn to scale.

(Table 1). These differences, particularly those of the head shape, gill arrangement, radula, and length of vas deferens, show that Bergh's *O. hystricina* belongs with the species *O. muricata* rather than the animal we have been commonly calling *O. hystricina*. This latter animal is in fact a new species, which I have described in this paper.

Discussion of *Diaphorodoris*

This new species, *Diaphorodoris* ***lirulatocauda,*** has been placed in the genus *Diaphorodoris* Ireland & O'Donoghue, 1923, because it has broadly based, triangular, denticulate teeth with no central tooth, an elongate body with a trailing keeled tail, a double-knobbed head, and a reproductive system similar to that of the type species *D. luteocincta* (M. Sars, 1870). Another important feature distinctive to this species is branchiae that are enclosed in a common sheath much as in the cryptobranch dorids, although in *Diaphorodoris* the branchiae are nonretractable as the sheath does not close over the branchiae. The genus *Diaphorodoris* was first created by IREDALE & O'DONOGHUE (1923) as a genus of Onchidorididae for the species *D. luteocincta,* although no distinctive characters were given. PORTMANN & SANDMEIER (1960) provide a history of the genus, redescription of the type species, and describe a new species, *D. papillata,* which varies only in color and tubercle shape from the type. Since then, no new species have been added and the generic status of *Diaphorodoris* is usually ignored. FRANC (1968) considers *Diaphorodoris* to be a subgenus, although he does not state of which genus. He places it in the family Lamellidoridae A. Pruvot-Fol, 1954, although the name Onchidorididae Alder & Hancock, 1845, has priority. THOMPSON & BROWN (1976) and THOMPSON (1976) place the species *luteocincta* in the genus *Onchidoris*. It is clear that in spite of the early arguments of PRUVOT-FOL (1932), the completeness of PORTMANN & SANDMEIER's (1960) description, and its recent use by SCHMEKEL & PORTMANN (1982), the establishment of *Diaphorodoris* as a distinct genus has not been universally accepted. I believe *Diaphorodoris* should retain its generic status. In support of this, I have summarized the important differences between the two genera in Table 2.

Table 2

Anatomical characters separating *Onchidoris* and *Diaphorodoris*.

	Onchidoris	*Diaphorodoris*
Shape	oval	elongate
Head	veliform	lobiform
Tail	not extending	trailing
Branchiae	separate pits enclosing tubercles	common sheath no tubercles enclosed
Radula	central present or absent	no central
Reproductive	vagina short bursa stalked receptaculum buried semiserial	vagina elongate bursa sessile receptaculum free vaginal

Comparison of Species in the Genus *Diaphorodoris*

Diaphorodoris ***lirulatocauda*** conforms closely to the morphology of *D. luteocincta.* It differs externally in having slimmer rhinophores, longer dorsal tubercles (0.6 versus 0.2 mm) and more branchial gills (7–9 versus 5–7). *Diaphorodoris luteocincta* normally has a yellow marginal ring and dorsal crimson blotching, but the red color is missing in the variety *alba* although the yellow ring is present. *Diaphorodoris papillata* can be distinguished from *D.* ***lirulatocauda*** by its red-colored, soft, inflated tubercles, which reach up to 0.8 mm in length. Internally *D.* ***lirulatocauda*** differs from the others by having an extra, reduced, outer external plate giving it the formula 2.1.0.1.2. In addition, the vas deferens of *Diaphorodoris* ***lirulatocauda*** is longer, with more coils, and the penis is armed with spines.

Diaphorodoris ***mitsuii*** (Baba, 1938) comb. nov.

The species *Lamellidoris* ***mitsuii*** (for which BABA, 1938, created a new subgenus *Lamellidorella* because it has an

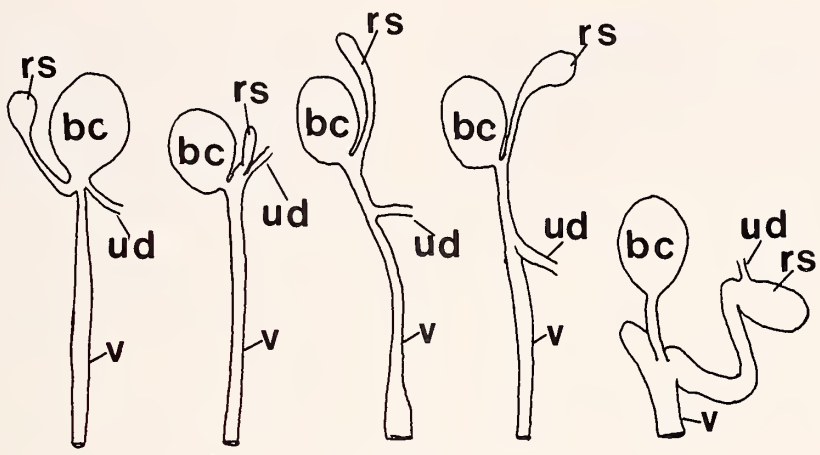

Figure 10

Reproductive systems—female portion. A. *Acanthodoris* from BERGH, 1880:pl. 13 (fig. 5). B. *Aciodoris* from BERGH, 1880:pl. 6 (figs. 18, 19). C. *Calycidoris* from ROGINSKAYA, 1972:pl. 1 (fig. 16). D. *Diaphorodoris*. E. *Onchidoris*. Not drawn to scale.

armed lip cuticle) must also be compared with the genus *Diaphorodoris*. The teeth have the same triangular, denticulate shape and lack a central plate. The body is also elongate with cylindrical tubercles and a trailing tail. Most importantly the branchiae are enclosed by a common cavity into which, according to BABA (1938, 1949), they can retract. This species has a rounded, double-lobed head like other *Diaphorodoris* species. The orange-yellow marginal ring is reminiscent of *D. luteocincta* var. *alba*. The small scales on the lip disk, which BABA regarded as distinctive (1938:131 [fig. 1B]), are similar to the small papillae on the lip cuticle of *D.* ***lirulatocauda.*** Unfortunately, the reproductive system of this species is not known, but externally, and according to its radular morphology, it appears to be conspecific with *Diaphorodoris*. I therefore designate it *Diaphorodoris* ***mitsuii*** (Baba, 1938) comb. nov.

Discussion of Generic Relationships in the Family Onchidoridiidae

One of the major characteristics separating *Diaphorodoris* and *Onchidoris* is that the branchiae do not possess separate pits, but emerge from a common cavity. This is similar to the branchial arrangement of cryptobranch dorids, although the gill pocket does not close over to protect the gills and thus the gill system can still be classified as nonretractile. Of the genera in the family Onchidoridiidae, *Aciodoris, Adalaria, Arctadalaria, Doridunculus, Onchidoris,* and *Prodoridunculus* have nonretractile branchiae that contract and are arranged in separate cavities. The genus *Acanthodoris* has gills that connect at their bases. However, the branchial margin of the acanthodorids indents between each gill and the gills usually enclose a tuberculated portion of the notum. *Calycidoris* and *Diaphorodoris* both have a single cavity containing gills that join at their bases. ROGINSKAYA (1972) proposed a new family, Calycidoridiidae, for the monotypic genus *Calycidoris* because its gills retract into a common sheath. However, in specimens that I examined it appears that the gill margin does not close over the gills and, thus, even when the gills are maximally contracted the system can still be considered nonretractile. The gills of *Diaphorodoris* ***mitsuii*** are probably similarly contracted, rather than retracted as claimed by BABA (1938, 1949). This branchial arrangement is very close to that of true cryptobranchs (which is termed retractile) differing only in that the gill margin does not close itself over the gills.

Diaphorodoris can be distinguished from *Calycidoris* by its broad, triangular-based, denticulate lateral teeth and its elongate body shape with a trailing, keeled tail. It is separated from other genera in the family Onchidoridiidae because its branchial gills are arranged in a common sheath. *Diaphorodoris* is more closely allied to the genera *Calycidoris, Acanthodoris,* and *Aciodoris* on the basis of the vaginal arrangement of the uterine duct than to *Onchidoris,* which has a semiserial arrangement (Figure 10). As in *Aciodoris,* the penis can be armed with spines. The radular teeth are most similar to some of the species in the genus *Onchidoris*. The elongate body shape, knobbed head, trailing keeled tail, common branchial pit, and vaginal arrangement of the copulatory bursa are all characteristics that validate the generic separation of *Onchidoris* and *Diaphorodoris*.

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